

Agronomic Performance and Multiple Disease Resistance in T2BS.2RL Wheat-Rye Translocation Lines

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ABSTRACT

Wheat (*Triticum aestivum* L.)-Rye (*Secale cereale* L.) T2BS.2RL translocations were shown to increase grain yield, resistance to biotic and abiotic stresses, and had minor effects on baking quality. The objective of this study was to test agronomic performance and resistance of a new wheat-rye translocation (T2BS.2RL, SLU) to powdery mildew (*Blumeria graminis* f. sp. *tritici* (DC.) E. O. Speer), leaf rust (*Puccinia triticina* Eriks.), stem rust (*Puccinia graminis* f. sp. *tritici* Eriks. & Henn.), stripe rust (*Puccinia striiformis* f. sp. *tritici* Westend.) and Hessian fly [*Mayetiola destructor* (Say)]. F₂ derived F₄-F₆ T2BS.2RL lines, non-translocation lines, and the wheat cultivar Holme were compared using intact seedlings or leaf segments. T2BS.2RL conferred seedling resistance to 17 powdery mildew isolates, 14 leaf rust and one stem rust pathotype. The T2BS.2RL lines were susceptible to 3 stripe rust pathotypes as seedlings, while showing adult plant resistance under natural conditions. Agronomic characters were compared in a 2-yr hill-plot field trial in Sweden. T2BS.2RL lines flowered 2 to 3 d later and had an increased number of spikelets per spike. The T2BS.2RL had no significant effect on yield, straw length, lodging, volume weight, 1000-kernel weight, fertility, α -amylase activity, or starch or protein content. The multiple disease resistance and the minor negative effects on agronomic performance of the T2BS.2RL, SLU translocation encourage its use in wheat breeding.

WHEAT-RYE CHROMOSOME translocations have been extensively used in wheat breeding, primarily as sources of disease resistance, but also to raise yield potential (Rabinovich, 1998). Genes for resistance against Russian wheat aphid (*Diuraphis noxia* Mordvilko) and green bug (*Schizaphis graminum* Rond.) infestation, and against powdery mildew (*Pm8*, *Pm17*), leaf rust (*Lr26*), stem rust (*Sr31*) and stripe rust (*Yr9*) infection have been transferred from chromosome 1RS into wheat in the

form of T1RS.1BL translocation lines (Singh et al., 1990; Friebe et al., 1996; Hsam and Zeller, 2002). The short arm of chromosome 1R also has a positive effect on the yield, stress tolerance, and adaption of wheat (Merker, 1982; Carver and Rayburn, 1994; Moreno-Sevilla et al., 1995; McKendry et al., 1996; Villareal et al., 1998; Kim et al., 2004). The expression of rye genes for resistance, protein content and grain yield in T1RS.1AL and T1RS.1BL translocation lines is dependent on both the origin of the rye and the genetic background of the wheat (Kim et al., 2004). However, most of the major disease resistance genes on 1RS have now been overcome by virulent pathotypes and the absence of wheat chromosome arm 1BS is detrimental to bread-making quality (Martin and Stewart, 1986; Dhaliwal et al., 1987; Koebner and Shepherd, 1988).

In contrast, wheat chromosome 2B appears highly suitable for alien gene transfers since it lacks any of the storage protein genes (gliadins or glutenins) that affect baking quality (Knackstedt et al., 1994). Genetic and physical mapping has shown that 2B and 2R are largely homeologous to one another, but homeologous recombination is restricted to the distal regions of the chromosomes (Lukaszewski et al., 2004). In particular, 2RL is genetically equivalent to 2BL, while 2RS shares homeology with both wheat 2BS and 6BS, and cannot fully compensate for the absence of either of them (Naranjo et al., 1987; Devos et al., 1993). The presence of 2R in wheat increases water-use efficiency and rooting characteristics (Lahsaiezadeh et al., 1983; Ehdaie et al., 2003), while the addition of 2RL significantly increases the content of kernel arabinoxylans, which are important for both baking and nutritional quality of cereals (Vinkx and Delcour, 1996; Boros et al., 2002). Genes for resistance to powdery mildew (Heun and Friebe, 1990), leaf and stem rust (Brunell et al., 1999), Hessian fly (Friebe et al., 1990; Sears et al., 1992; Lee et al., 1996), and tolerance to barley yellow dwarf virus (Nkongolo and Comeau, 1998) have all been located to chromosome 2R. The presence of resistance genes, promising quality characters and the good agronomic performance associated with 2RL make this chromosome arm an attractive target for wheat improvement.

The T2BS.2RL translocation from Chaupon rye in wheat cultivar Hamlet (PI 549276) was identified in a regenerant from tissue culture and found to carry a single dominant gene (*H21*) for Hessian fly resistance (Sears et al., 1992; Hatchett et al., 1993). Investigations of the milling and baking properties of the Hamlet translocation line found a slight reduction in test weight, flour yield, kernel hardness, mixograph-mixing time, and bake-

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Published in Crop Sci. 47:254–260 (2007).

Crop Breeding & Genetics

doi:10.2135/cropsci2006.04.0269

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Abbreviations: GISH, genomic in situ hybridization.

mixing time; and a slight increase in flour color and water absorption that could be overcome by selecting for earliness (Knackstedt et al., 1994). A T2AS.2RL (Imperial rye) translocation in the wheat cultivar Chinese Spring was superior to normal Chinese Spring with respect to grain yield, shoot biomass at maturity, root biomass, and water use efficiency (Lahsaiezadeh et al., 1983; Ehdaie et al., 1991, 1998). The presence of the Hamlet T2BS.2RL in cv. Pavon and Karl wheat backgrounds delayed maturity, while the effects on number of seeds per spike, grain yield and harvest index were background-dependent (Fritz and Sears, 1991; Ehdaie et al., 2003).

The objective of the present study was to investigate the effects of a new wheat-rye T2BS.2RL translocation (T2BS.2RL, SLU). We report the outcomes of experiments testing the resistance to powdery mildew, leaf rust, stem rust, stripe rust, Hessian fly, and agronomic performance, and discuss its potential for wheat improvement.

MATERIALS AND METHODS

Plant Materials

A T2BS.2RL, SLU translocation line was isolated from crosses between normal winter wheat cultivars Holme and Kraka and a double disomic substitution line in which 1R and 2R replaced, respectively, 1B and 2B (Merker and Forsström, 2000). The homozygous T2BS.2RL, SLU translocation carrier was crossed with cv. Holme. Lines homozygous for either the presence or absence of the T2BS.2RL, SLU translocation were isolated in F₂ and F₃ generations, by means of mildew resistance response tests and chromosome C-banding (Merker and Forsström, 2000). Each line described in the present study is descended from a different F₂ plant. F₂ derived F₄–F₆ lines were used to compare translocation lines (i.e., lines homozygous for the T2BS.2RL translocation), and non-translocation lines (i.e., lines without the translocation, homozygous for chromosome 2B). All the lines are fully fertile and have normal seed-set. Chromosome C-banding and genomic in situ hybridization (GISH) were used to detect the presence or absence of T2BS.2RL in the lines used for determining disease and pest resistances. Cultivar Holme was used as a universal control.

International sets of differential tester lines carrying specific genes for disease resistance were used to compare the infection type patterns of translocation and non-translocation lines with identified genes. The cv. Chancellor powdery mildew (*Pm*) near-isogenic lines, and TP114/2*Starke for *Pm6*, are maintained at Lehrstuhl für Pflanzenbau, Freising-Weihenstephan, Germany. The North American and Mexican leaf rust (*Lr*) resistance tester lines and International, North American, and Australian stem rust differentials (McIntosh et al., 1995) are maintained at CIMMYT, Mexico. The International, European, Australian, and North American stripe rust (*Yr*) differentials (McIntosh et al., 1995) are maintained at the John Innes Centre, UK. The check lines H3, H5, H6, H7H8, and cv. Hamlet used in the Hessian fly experiment are maintained at USDA/ARS Dep. of Entomology, Purdue University, West Lafayette, U.S.A.

Powdery Mildew Experiments

Detached seedling leaf segment tests of translocation, non-translocation lines and cv. Holme were conducted with 17 European powdery mildew single-spore isolates (No. 2, 5, 6, 9, 10, 12, 13, 14, 15, 16, 17, 70, 72, 76, 90, 98, and 117) with virulence against combinations of the major resistance genes

Pm1a, *Pm1b*, *Pm1c*, *Pm2*, *Pm3a*, *Pm3b*, *Pm3c*, *Pm3d*, *Pm3e*, *Pm3f*, *Pm4a*, *Pm4b*, *Pm5a*, *Pm5b*, *Pm6*, *Pm7*, *Pm8*, *Pm9*, *Pm17*, *Pm19*, *Pm22*, and *Pm29* (Hsam and Zeller, 2002). The isolates are maintained at the Lehrstuhl für Pflanzenbau, Freising-Weihenstephan, Germany. Seedling tests were performed on primary leaf segments maintained on 6 g/L agar with 35 mg/L benzimidazole. Each set of leaf segments was inoculated with one single-spore isolate at a time. The methods of inoculation and conditions of incubation followed Lutz et al. (1995). Ten plants of each line were used in two-three replications for each isolate. Infection types were recorded 10 d after inoculation using a scale of 0 to 9, where 0 = no visible disease symptoms and 9 = 50 to 100% leaf area covered with sporulating colonies (Heun and Friebe, 1990). Greenhouse tests were performed to determine the effectiveness of resistance at the adult plant stage. Three seedlings from each line and replication were grown to maturity and subjected to the highly virulent, naturally occurring powdery mildew pathotypes present in the greenhouse at Lehrstuhl für Pflanzenbau, Freising-Weihenstephan, Germany. The percentage infected leaf area on the penultimate leaf (F-1 leaf) was first assessed 2 wk after flowering, and thereafter every week until maturity.

Leaf Rust Experiments

The reaction to leaf rust infection was tested on intact seedlings of translocation, non-translocation lines, and cv. Holme using six Mexican pathotypes, and on detached seedlings using eight European single-spore isolates. The Mexican pathotypes CCJ/SP, MBJ/SP, MCJ/QM, MCJ/SP, TBD/TM, and TCB/TD carrying different combinations of virulence against *Lr1*, *Lr2a*, *Lr2b*, *Lr2c*, *Lr3*, *Lr3bg*, *Lr10*, *Lr11*, *Lr12*, *Lr13*, *Lr14a*, *Lr14b*, *Lr15*, *Lr17*, *Lr18*, *Lr20*, *Lr22a*, *Lr22b*, *Lr23*, *Lr26*, *Lr27+31*, *Lr28*, *Lr34*, *Lr35*, *Lr37*, and *LrB*, are maintained at CIMMYT, Mexico. The European single-spore isolates S-12, S-28, S-29, S-48, S-71, Pt-8, Pt-9, and Pt-60 with combinations of virulence against *Lr1*, *Lr2a*, *Lr2b*, *Lr2c*, *Lr3*, *Lr3bg*, *Lr3ka*, *Lr10*, *Lr11*, *Lr12*, *Lr13*, *Lr14a*, *Lr14b*, *Lr15*, *Lr16*, *Lr17*, *Lr18*, *Lr20*, *Lr21*, *Lr22a*, *Lr22b*, *Lr23*, *Lr26*, *Lr27+31*, *Lr28*, and *Lr34*, are maintained at the Lehrstuhl für Pflanzenbau, Freising-Weihenstephan, Germany. Ten intact 10-d-old seedlings per line were challenged with each pathotype, by spraying with urediniospores suspended in the light-weight mineral oil Soltrol 170 (Phillips 66, Bartlesville, OK) (2–3 mg/ml). Inoculated plants were incubated in a dew chamber overnight at 18 to 20°C and then transferred to greenhouse chambers at 18 to 22°C, with 16 h of daylight (Singh and Rajaram, 1991). The detached leaf segment tests followed the methods of Lutz et al. (1995), except that after inoculation, the material was held in a dark, humid chamber overnight. The tests were conducted with 10 to 12 plants per line in two replications. Infection types were recorded 9 to 12 d after inoculation, using a scale of 0 to 4 similar to that described by Stakman et al. (1962) where 0 to 2 is considered resistant to moderately resistant, and 3 to 4 moderately susceptible to susceptible.

Stem Rust Experiment

The Mexican stem rust pathotype RTR with virulence against *Sr5*, *Sr6*, *Sr7a*, *Sr7b*, *Sr8a*, *Sr8b*, *Sr9a*, *Sr9b*, *Sr9d*, *Sr9f*, *Sr9g*, *Sr11*, *Sr12*, *Sr15*, *Sr16*, *Sr19*, *Sr20*, *Sr21*, *Sr23*, *Sr28*, *Sr34*, *Sr36*, *SrPI*, is maintained at CIMMYT, Mexico. A set of 10 8-d-old seedlings of translocation, non-translocation lines, cv. Holme, and tester lines were inoculated by spraying with urediniospores suspended in Soltrol 170, placed in a dew chamber overnight at 18 to 20°C, and transferred to a greenhouse at 18 to 22°C. Infection types were scored after 12 to 14 d based on a scale of 0 to 4 for stem rust (Singh, 1991) where 0 to 2 is con-

sidered resistant to moderately resistant, and 3 to 4 moderately susceptible to susceptible.

Stripe Rust Experiment

An equal parts mixture of the European stripe rust isolates WYR 94–519, WYR 96–17 and WYR 96–502 with virulence against *Yr1*, *Yr2*, *Yr3*, *Yr4*, *Yr6*, *Yr9*, and *Yr17* were used to evaluate resistance in the translocation, non-translocation lines, and cv. Holme. To break the dormancy of the urediniospores stored over liquid nitrogen, the inoculum was held at 40°C for 5 min. The urediniospores were mixed with an equal volume of talcum powder and air sprayed on to 10 10-d-old seedlings per line and tester line, which had been pre-sprayed with ddH₂O containing a few drops of Tween 20 (Sigma Chemical Company, St. Louis, MO) as a wetting agent. The inoculated plants were placed in a dark incubator room at 10°C and 95% humidity for 24 h to optimize spore germination and then transferred to a containment greenhouse at 15/18°C and 16/8 h day/night cycle. Infection types were recorded 12 to 14 d after inoculation, using a scale of 0 to 4 (McIntosh et al., 1995) where 0 to 1 is resistant, 2 moderately resistant, and 3 to 4 susceptible (Boyd and Minchin, 2001).

Hessian Fly Experiment

Translocation, non-translocation, cv. Holme, and tester lines were evaluated for reaction to Hessian fly biotype L and biotype E maintained at USDA/ARS Dep. of Entomology, Purdue University, West Lafayette, U.S.A. The tests were performed using a set of 10 to 20 individuals per line according to procedures described by Hatchett et al. (1981) and Foster et al. (1988). Individual plants were scored for reaction to larval feeding 10 to 14 d after infestation. Susceptible plants were stunted, blue-green and had broad second and third leaves. Resistant plants retained their normal height and color.

Field Experiments

Field trials were conducted in Alnarp, southern Sweden, over 3 yr (2001, 2002, and 2003). Hill plots consisting of 15 plants per plot were sown in trays in the greenhouse, vernalized for 10 wk at 2 to 4°C and planted in a randomized complete-block design in the field in spring. In all, 85 T2BS.2RL line hill plots, 72–73 non-translocation line hill plots, and 21 cv. Holme hill plots were assessed. The spacing between hill plots was 110 cm and the trial was surrounded by a row of winter wheat cv. Kosack. The field was fertilized with NPK and micronutrients (75 kg N/ha) immediately after planting. In 2001 and 2003, the trial was treated with 1 L/ha of Tilt Top 500 EC (cis-4-[3-(4-tert-butylphenyl)-2-methylpropyl]-2,6-dimethylmorpholin and 1-[2-(2,4-diklorfenyl)-4-propyl-1,3-dioxolan-2-yl-metyl]-1H-1,2,4-triazol) (Makhteshim-Agan, Leusden, Holland) to control fungal infection. During 2002, no fungicide treatment was given, exposing the trial to a natural stripe rust epidemic. Because of severe damage to non-translocation carrier lines and cv. Holme, only the data from years 2001 and 2003 were analyzed for agronomic performance.

The following parameters were recorded for each hill plot: grain yield per hill plot (g); heading time (days after half the spikes of the first hill plot had emerged); straw length (cm); lodging (100% = fully upright); grain volume weight (kg/hl); 1000-kernel weight (g); spike size (number of spikelets per spike) and fertility (number of seeds per spikelet of one well developed spike). Grain α -amylase activity was measured according to Bernfeld (1951) for the 2003 trial. Starch and protein concentration (%) was determined for the 2001 trial on a

dry weight basis, according to ICC methods, by the Swedish Cereal Laboratory, Svalöf Weibull AB, Svalöv, Sweden.

Analyses of variance were performed for each character measured for each year and combined across years using General Linear Modeling (Minitab Release 14 statistical program). The datasets were normally distributed, except for lodging, as there was no variation in this character. *t* tests were used for mean comparisons.

Coleoptile Color Experiment

During vernalization, variation for seedling (red/green) coleoptile color was observed, and an experiment was conducted to study this trait. Ten seeds per each of 26 translocation, 21 non-translocation, and 6 cv. Holme hill plots harvested during the year 2003, were germinated on Wettex paper (FHP Vileda Professional, Liege, Belgium) for 3 d in a growth chamber at 19°C and transferred to an unheated greenhouse chamber 2 to 5/0°C and 10/14 h day/night cycle. After 11 d, the coleoptiles were 1–2 cm high and the color was recorded.

RESULTS AND DISCUSSION

Disease and Pest Resistance

The infection types of the differential tester lines corresponded to expected results (Singh, 1991; Singh and Rajaram, 1991; McIntosh et al., 1995; Hsam and Zeller, 2002) except for powdery mildew isolate no. 17 which was virulent against *Pm8*. The results from all the disease and pest resistance experiments are summarized in Table 1. The lines carrying the T2BS.2RL, SLU translocation were completely resistant to all 17 powdery mildew isolates at the seedling stage and to the mixture of isolates at the adult plant stage. The leaf rust and stem rust experiments showed similar results, although infection types in the translocation carriers were consistently higher when challenged with the Mexican leaf rust pathotypes than with the European leaf rust single-spore isolates, most likely because of different experimental methods (intact seedling vs. leaf-segment method). The non-translocation carrier lines and cv. Holme were susceptible to all the powdery mildew and rust pathotypes used in the study. Thus the genetic basis of the resistance in the T2BS.2RL, SLU translocation is almost certainly ascribable to gene(s) located on the 2RL rye segment. The highly consistent infection types produced by the different translocation lines showed that the resistance to powdery mildew, leaf rust, and stem rust was independent of genetic background.

In contrast, the T2BS.2RL, SLU translocation did not confer seedling resistance to any of the European stripe rust isolates, showing the same infection types as the non-translocation lines and cv. Holme. Preliminary results from adult plant experiments using the same isolate mixture does however suggest that the T2BS.2RL, SLU confers adult plant resistance to stripe rust (resistant to moderately resistant) compared to the non-translocation lines and cv. Holme (moderately resistant to susceptible) (unpublished results, 2004). This result is consistent with our 2002 field observations, when no fungicide was applied. In the presence of a heavy natural stripe rust epidemic, the translocation carriers were resistant to mod-

Table 1. Comparison of seedling and adult plant resistance (APR) to powdery mildew (Pm), leaf rust (Lr), stem rust (Sr), stripe rust (Yr) and Hessian fly (HF) in T2BS.2RL translocation and non-translocation lines, and wheat cultivar Holme.†

Character	T2BS.2RL translocation			Non-translocation			Holme	
	Mean	Range	No	Mean	Range	No	Mean	No
Pm isolates from Europe (17 isolates) seedling	0	0–1	10	8	7–9	10	8	1
Pm pathotypes from Europe (mix) APR	0	0	10	15%	5–25%	10	5	1
Lr isolates from Europe (8)	; 1	; – 1	10	4	3–4	10	4	1
Lr pathotypes from Mexico (6)	X	; 1 – X	5	3+	3C3–3+	5	3+	1
Sr pathotype from Mexico (1)	X	X	5	3+	3+	5	3+	1
Yr pathotypes from Europe (mix of 3) seedling	4	3–4	4	4	4	2	4	1
HF North American Biotype L	4/10	0–8/9–15	7	0/15	0/12–18	5	0/18	1
HF North American Biotype E	0/18	0–1/16–19	7	0/16	0/10–18	5	0/19	1

† No = number of lines (10–20 plants per line) used in the experiments. Powdery mildew seedling experiments were scored on an infection type scale from 0–9 where 0 = no visible signs of infection, 1 = small pustules and necrotic flecks, 7–9 = 50–100% leaf area covered with mycelium; Powdery mildew APR was scored as percentage infected leaf area; Leaf rust and stem rust experiments were scored on a scale from 0–4 where 0 = no uredinia or other macroscopic signs of infections, ; = no uredinia, but hypersensitive necrotic or chlorotic flecks of varying size present, 1 = small uredinia often surrounded by necrosis, 3 = medium-sized uredinia that may be associated with chlorosis or rarely necrosis; 4 = large uredinia without surrounding chlorosis; X = random distribution of variable-sized uredinia on single leaf, + = uredinia somewhat larger than normal for the infection type, C = more chlorosis than normal; Stripe rust experiment was scored on a scale from 0–4 where 0 = no uredinia or other macroscopic signs of infections, 3 = sporulation with chlorosis; 4 = abundant sporulation without chlorosis; Hessian fly resistance was scored as number of resistant plants/number of susceptible plants using 10 to 20 plants per line.

erately resistant, while non-translocation carriers were heavily infected (Merker and Hysing, 2003). The stripe rust infection damaged agronomic performance to such an extent in the susceptible lines that this field trial had to be excluded from the present analysis. Cultivar Holme appears to carry some adult plant resistance to stripe rust, and the putative adult plant resistance located on the 2RL segment must therefore be further studied in a stripe rust susceptible wheat background.

Carriers of the T2BS.2RL, SLU translocation were susceptible to the two Hessian fly biotypes used in the study. This differs from the T2BS.2RL, Hamlet translocation which confers complete resistance to biotype L, which has the widest virulence range of the known biotypes (Hatchett et al., 1993), and presumably reflects variation in allelic content of the two independent rye sources.

Powdery mildew and rusts are economically destructive diseases of common wheat in many areas of the world (Roelfs et al., 1992; Hsam and Zeller, 2002). Resistance is one of the most effective, environmentally sound, and economic means of control (Pink, 2002). However, new pathogen races rapidly overcome most race-specific resistance genes and there is a continuous need to identify and incorporate effective resistance into new wheat cultivars. Although no race of powdery mildew, leaf rust, or stem rust was identified to be virulent on T2BS.2RL, SLU translocation carriers, any widescale use of the translocation would likely result in the breakdown of the resistance, as has occurred for the 1RS resistance complex (*Pm8-Lr26-Sr31-Yr9*) in the T1BS.1RL translocation. A breeding strategy combining the T2BS.2RL, SLU translocation with several effective resistance genes (pyramiding) in cultivars with high levels of partial (quantitative) resistance (McDonald and Linde, 2002; Wang et al., 2005) should promote the durability of resistance.

Agronomic Performance

The combined ANOVA (data not shown) indicated significant differences in means for heading date, straw length, lodging, grain volume weight, spike size, and fertility between years. However, because no significant change in the rank order of groups (translocation, non-

translocation and cv. Holme) was observed in any year, the means across years are reported in Table 2. Significant differences within lines seen for the agronomic traits are common in hill-plot designs, and were probably caused by climatic factors, different genetic backgrounds, and interactions of genetic backgrounds with the translocation chromosome. The consistent infection types in the disease resistance experiments, however, indicated no, or at most minor, effects due to differences in genetic background within translocation and non-translocation lines.

No significant difference was found between non-translocation lines and control cv. Holme for any of the characters examined, showing that there was no effect due to the wheat-background. Therefore, any significant difference between the translocation and non-translocation groups could be ascribed to the presence of the T2BS.2RL translocation. The presence of the T2BS.2RL, SLU significantly increased the number of spikelets per spike (+12%), possibly because of the significantly delayed heading by 2 to 3 d compared to non-translocation lines and cv. Holme. There was no significant difference between the translocation, non-translocation lines, and cv. Holme for grain yield, straw length, lodging, grain volume weight, 1000-kernel weight, fertility, grain α -amylase activity, or grain starch and protein content (Table 2).

The Hamlet T2BS.2RL translocation delays maturity and increases the number of seeds per spike (Fritz and Sears, 1991; Ehdaie et al., 2003). Similarly, the T2BS.2RL, SLU translocation delays heading and increases the number of seeds per spike via a positive effect on the number of spikelets per spike (Table 2). The Hamlet T2BS.2RL translocation in wheat cv. Karl increases grain yield, aerial biomass at maturity, seeds per spike, and seeds per plant, but delays maturity, and reduces grain weight and harvest index (Fritz and Sears, 1991). Its presence in wheat cv. Pavon reduces the number of spikes and delays maturity, but has no effect on either harvest index or grain yield (Ehdaie et al., 2003). This inconsistency shows that the effect of the Hamlet T2BS.2RL is background dependent and operates via a genetic interaction between genes on the 2RL segment

Table 2. Comparisons of means and standard deviations (SD) of agronomic performance for T2BS.2RL translocation and non-translocation lines, and wheat cultivar Holme grown at Alnarp, Sweden 2001 and 2003.

Character	T2BS.2RL translocation			Non-translocation			Holme		
	Mean	SD	No	Mean	SD	No	Mean	SD	No
Yield per hill (g)	61.3	29.7	85	61.1	30.7	73	56.6	31.5	21
Heading (days after first hill) [†]	8.2 a	2.9	85	5.6 b	2.8	73	5.8 b	3.0	21
Straw length (cm)	93.1	10.2	85	92.3	9.6	73	88.3	9.1	21
Lodging (%)	98.4	4.6	85	97.5	4.6	73	100.0	0.0	21
Grain volume weight (kg/hl)	75.5	4.4	85	73.7	5.1	73	72.9	5.2	21
Thousand kernel weight (g)	37.4	4.5	85	37.3	5.4	72	36.6	5.4	21
Spike size (spikelets/spike) [†]	24.0 a	2.7	85	21.4 b	2.5	73	20.1 b	2.8	21
Fertility (seeds per spikelet)	3.1	0.5	85	3.1	0.3	73	3.1	0.3	21
Grain alpha amylase activity (μmol/mg)	1.0	0.3	37	0.9	0.3	48	0.9	0.3	12
Grain starch content (%)	66.8	1.4	38	67.0	1.0	34	67.1	2.0	10
Grain protein content (%)	16.5	1.4	38	15.0	1.2	34	16.0	1.8	10
Coleoptile color	Red	–	26	Green	–	21	Green	–	6

[†] Significantly different from the mean of the non-translocation lines at $p = 0.05$ based on t test; values with the same letter in the same row do not differ significantly at $P < 0.05$.

and those elsewhere in the wheat genome. In contrast, the agronomic effects of 1RS on cv. Pavon 76 reflected differences between rye origins rather than an interaction between rye and wheat genes (Kim et al., 2004).

Homologous recombination between alien chromosome segments transferred to wheat represents a strategy for increasing variation and for incorporating new genes for disease and pest resistance. Thus, for example, Mater et al. (2004) combined the powdery mildew resistance from the 1RS segment of a T1RS.1BL translocation with green bug resistance from the 1RS segment in a T1RS.1AL translocation. A further strategy lies in shortening the segment by de novo translocation and/or recombination. Thus, Friebe et al. (1994) were able to stabilize the powdery mildew resistance present in a monosomic 6RL(6D) substitution line by selecting a T6BS.6RL translocation chromosome. Similarly, the usefulness of the present T2BS.2RL, SLU and other T2BS.2RL translocations could be enhanced by recombination between different 2RL segments to combine pest and disease resistance in an agronomically desirable wheat background.

Molecular markers for 2RL segments from various rye sources, based on Random Amplified Polymorphic DNA (RAPD) (Seo et al., 1997; Brunell et al., 1999), moderately repetitive rye DNA (Lee et al., 1996), Amplified Fragment Length Polymorphism (AFLP) (Seo et al., 2001) and conversion of Random Fragment Length Polymorphism (RFLP) probes to Sequence Tagged Site (STS) markers (Forsström et al., 2003) have been described. These can be used to efficiently identify and track the rye segment in breeding programs. In this study, the result of the coleoptile color experiment showed that the translocation lines develop a deep red coleoptile color compared to the green or occasionally pink color of non-translocation lines and cv. Holme, allowing this trait to be used as a simple morphological marker. The presence of a coleoptile color gene(s) on chromosome 2R was proposed by Melz and Thiele (1990), but the red phenotype could also be caused by the absence of suppressors of anthocyanin pigments on the long arm of wheat chromosome 2B (Sutka, 1977). However, the stability of the marker has yet to be investigated, and its expression may be modulated by temperature and/or be dependent on

the wheat background. The ability to genetically map 2RL using microsatellites and other marker types (Khlestkina et al., 2004; Camacho et al., 2005) may facilitate further studies and mapping of valuable genes in wheat-rye translocations.

In conclusion, the results of the present study on the T2BS.2RL, SLU translocation and studies on the Hamlet T2BS.2RL translocation (Hatchett et al., 1993; Knackstedt et al., 1994; Ehdaie et al., 2003) show that these translocations have a positive effect on yield, little influence on baking quality, and variable useful disease and pest resistances that could contribute to wheat improvement. The use of molecular markers in conjunction with genetic recombination between different rye 2RL segments in a wheat background would open the way to genetically define the useful genes present in this rye chromosome arm.

ACKNOWLEDGMENTS

We thank Maria-Luisa Prieto-Linde of the Swedish University of Agricultural Sciences, Ruth McCormack of John Innes Centre, Agnese Kolodinska-Brantestam of the Nordic Gene Bank, and Linda Wernersson, for their excellent technical assistance.

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